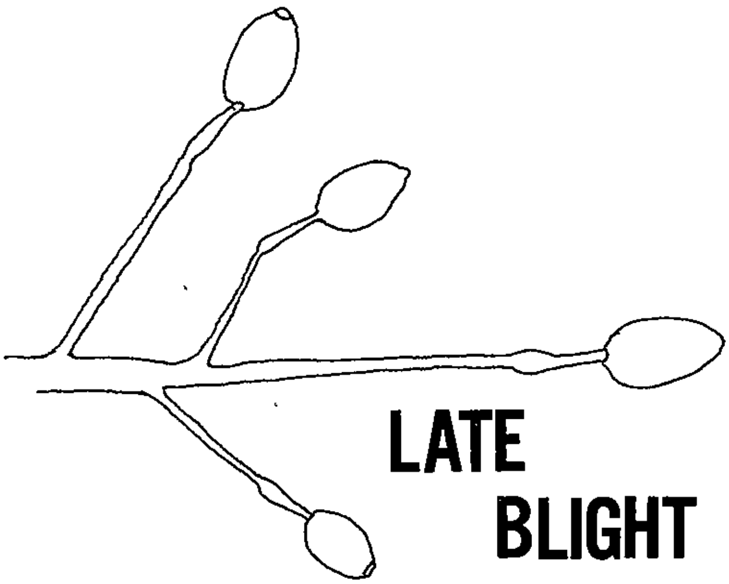
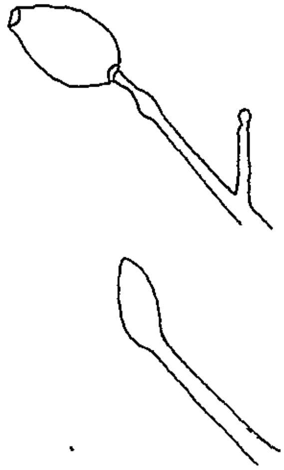
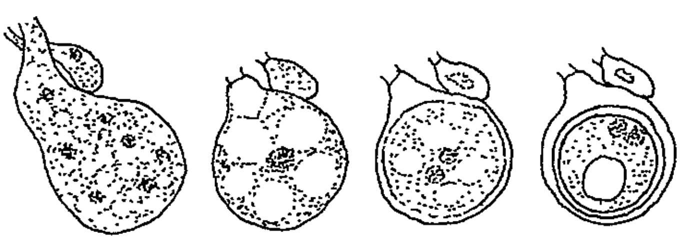
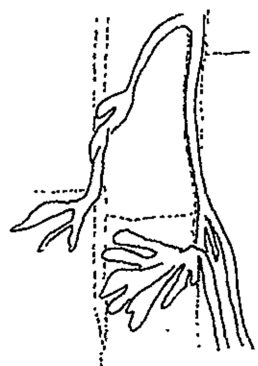




# LATE BLIGHT STRATEGY

## REPORT OF THE INTERNATIONAL POTATO CENTER'S LATE BLIGHT PROJECT PLANNING CONFERENCE





after Elizabeth Blackwell


**CENTRO INTERNACIONAL DE LA PAPA**

(International Potato Center) La Molina

Apartado 5969, Lima - Peru

# INTERNATIONAL POTATO CENTER (CIP)

REPORT OF THE

LATE BLIGHT PROJECT PLANNING CONFERENCE

Held at CIMMYT - El Batán, Edo. de México, MEXICO

AUGUST 22-27, 1973

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## FOREWORD

The International Potato Center seeks the advice of world experts to establish its objectives. To set its overall objectives it called on a large group of scientists who participated in "An International Symposium on Key Problems and Potentials for Greater use of the Potato in the Developing World" held at Lima during July 17 to 19, 1972 (the proceedings of which were published under the title Prospects for the Potato in the Developing World). To define the more precise objectives of the principal projects of the Center, project planning conferences in which about 10-12 scientists(including some CIP staff members) have been organized. To date the following have been held: Bacterial Wilt Project Planning Conference, San José de Costa Rica, December 10-12, 1972; Taxonomy Workshop, a review and planning conference for the systematic collection and classification of potato germ plasm, held at CIP, January 4-15, 1973; and the Late Blight Project Planning Conference, held at CIMMYT, El Batán, México, during August 22-27, 1973, the results of which are reported herein. Reports of previous conferences and workshops are also available. Future conferences of this type to be held are to be on: Nutritional Quality, November 1973; Nematode Resistance, February 1974; Cold Resistance, February 1974; Utilization of Genetic Resources, April 1974; Seed Production Technology for Developing Countries, September 1974; Potato Utilization in Farming Systems, Processing and Storage, February 1975; and Adaptation of the Potato to the Lowland Tropics (to include bacterial wilt, late blight and physiology), September 1975. During these conferences, work projections for CIP Staff and coordination with other scientists is programmed for a five year period, but the topic is to be reviewed again at a similar conference every three years.

A Background Paper for the conference reported herein was prepared by Dr. Vilhelm Umaerus of the Swedish Seed Association, and is reproduced as Appendix I - Background Paper for the Late Blight Project Planning Conference of CIP. Dr.Umaerus was Chairman of the conference, with different participants acting as discussion leaders and secretaries for the sessions. All participants helped in writing and correcting this report; Dr. O. T. Page, on sabbatic leave from his post as Head of the Biology Department at the University of New Brunswick, assisted in the final editing done by CIP staff. The final section "Proposed Program", encompasses the recommendations that appear in prior sections that the Center staff considers itself capable of executing or coordinating.

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Back row: Drs. Mooi, Niederhauser, Black, Umaerus, Thurston, Malcolmson and Wurster.
Front row: Drs. French, Sayre, Romero, Gallegly, Yamamoto, Guzmán and Galindo.

Dr. David Thurston shows off an andigenum clone that is resistant to late blight at CIP's testing ground at Atizapán, Toluca Valley, Mexico.

## INTRODUCTION

Late blight of potato has been the most feared and destructive disease of this basic food crop since the disease was discovered more than a century ago. It is among the most important of all plant diseases and perhaps has received as much attention through research and extension as any. In spite of the great state of knowledge concerning it, late blight remains as a major problem for control in developed countries, and, more importantly, as a limiting factor in potato production in the emerging nations, the target for the major thrust of the International Potato Center.

The causal fungus, Phytophthora infestans (Mont.) de Bary, is biologically adapted to thrive in most environments where the potato is cultured. It is well adapted for widespread dissemination through the air or through movement of infected tubers of its host. The infected tuber is the major source of survival in developed countries, whereas in developing countries the continuous overlapping culture of the potato and tomato serves as an additional important means of survival.

Disease control measures include such practices as destruction of discarded infected tubers and volunteer plants, regulatory laws requiring seed tubers and tomato transplants to be free of disease, protection of foliage by application of fungicides, and the use of resistant varieties. Fungicidal control has developed to a high state of technology in many nations. The modern fungicidal chemicals and sophisticated but expensive machinery provides effective control in most developed nations. In some, resistant varieties are being introduced whereas in other developed nations resistant varieties have not been accepted because of inferior tuber quality or because the type of resistance available is not effective in the face of new races of the pathogen.

In many developing nations there is relatively little use of fungicides. Most of the culture in these countries consists of small plantings by subsistence farmers. Effective modern spray machines are usually too expensive and are not designed for use in this type of culture. Hand sprayers are used by some small growers but control is unsatisfactory in the rainy seasons when the potato is usually grown in tropical countries. More importantly, the subsistence farmer seldom has money to purchase sprayers and fungicides where they are available.

It thus remains that the greatest promise for control of potato late blight in developing countries lies with the introduction of resistant varieties. The knowledge that high levels of resistance to all known races of the pathogen are available gives confidence that this promise can become a reality. It is the firm belief of this planning group that the program of CIP for control of late blight should be aimed directly toward the establishment of stable resistant varieties in developing nations. This report summarizes our view of the present status of resistance to late blight and recommends a research and development program which we believe can significantly reduce the importance of late blight in developing nations in a relatively short period, and provides for the development of the

scientific base necessary for continued improvement in the future.

## RESISTANCE TO LATE BLIGHT

### Status of Knowledge

Research leading to the current state of knowledge of late blight has revealed that two genetic systems control host resistance to the disease. The system giving hypersensitive resistance is controlled by a series of at least eleven genes (R-genes) derived from S. demissum, each independently inherited as a simple Mendelian character with resistance being dominant. History has well recorded that as fast as these genes have been isolated individually or recombined in S. tuberosum clones, the fungus has produced new races to completely overcome them. It is obvious that this type of resistance alone will be of little or no value for stable resistance to late blight in developing countries.

The other genetic system is controlled by a series of multiple genes which appear to be additive in effect and inherited in a polygenic fashion. This has been termed 'field resistance' and is apparently stable in the face of the variable pathogen. It consists of a complex of factors including resistance to entrance of the fungus, resistance to growth of the parasite, and sporulation capacity, although additional factors play a role in field resistance. Field resistance is race non-specific. It is strongly influenced by physiological and environmental factors. This type of resistance offers much hope in international control of late blight.

Since field resistance is controlled by many factors, rather than one or two, the fungus is probably unable to adapt itself to cultivars possessing this kind of resistance, at least not easily for field resistance appears to be stable so far. Observations in Kenya and Colombia indicate that no change has occurred even after 20 years of cropping twice a year. In Mexico, however, some suggestions of possible increase of the pathogen's ability to overcome field resistance are present among Mexican cultivars; thus the variety Atzimba appears to be more susceptible than when it was selected. In addition, records of blight incidence from fungicide treated and untreated plots of many years ago, and those recently recorded, indicate that some clones may be slightly more affected. The possibility that a shift towards a greater capacity of the late blight fungus to overcome field resistance is taking place is of concern for the development of resistant varieties.

Little is known about the levels of resistance needed in the developing world, the adaptability of resistant selections to different growing conditions, and the influence of these conditions on the expression of field resistance. Standard differential host sets for field resistance, and for R-genes, would be useful tools to gain this needed information, as also is the development of standard disease assessment methods for comparisons of late blight readings in different locations and for differing purposes (breeding, variety testing, studies on late blight epiphytotics and on the mechanisms of resistance).

Although much has been learned about the mode of action of field resistance, the true nature of resistance is not understood. Further studies on the mechanisms of resistance and inheritance of resistance with emphasis on their different components would be of much benefit for the development of late blight resistant varieties. Such studies should be intensified and can probably be most efficiently done through linkage projects or by visiting scientists and post-doctoral fellows.

Currently foliage resistance is recognized as the most important goal to achieve for late blight control in developing countries. However, tuber resistance should not be neglected and a better understanding of various aspects of tuber resistance is needed. Tuber susceptibility should be taken into account in selection work at time of maturity. For the problem of tuber susceptibility consideration should be given to cultural practices that may be easier to achieve by subsistance farmers than in large scale farming (good covering of hills, early haulm destruction, rejection of infested tubers before storage). Cultural practices may at present be sufficient to reduce the effect of tuber damage; these can be taught through outreach activities. With improved technology in the future potato production for the consumer will require greater attention to tuber problems. The question of whether or not tuber and foliage resistance is correlated is perhaps the most important.

There has been recent concern that high levels of teratogenic and gastroenteric compounds in tubers is correlated with high resistance to late blight, but this concern is now lessening as new data is generated. CIP staff should keep informed about work on teratogenic and other substances of suspected toxicity to humans that may be found in blighted tubers. Since it is quite evident that high levels of glycoalkaloid compound in tubers will cause food poisoning symptoms selections and varieties used as parents in a breeding program should be assayed for these compounds.

Proposed Program

Efforts should be made to initiate a long term project of international scope to determine the "stability" of field resistance. Various approaches may be needed to recognize shifts in pathogenicity (aggressiveness) and if it occurs, explanations for it must be found.

Two standard differential host sets should be established, one for field resistance and another for the R-genes, and virus-free tubers of these should be produced for international distribution.

The criteria for selection of the set for field resistance should be: 1) R-genes should be avoided as much as possible; 2) The range in level of resistance should coincide with the 1 to 5 grades of the rating system in Mexico and also include supplemental entities to represent the temperate region response, so as to be able to interpret the results of work in these regions to the advantage of the developing world; 3) Include different maturity levels (this may be covered under the previous criterion); 4) Incorporate stem blight considerations; and 5) Incorporate different combinations of components of field resistance when identified.

The criteria for selection of a set for R-genes should be: 1) Avoid field resistance as much as possible. The series at Pentlandfield ($R_1$ to $R_4$) has been agreed upon as an initial base. 2) Use such single gene genotypes ($R_1 - R_{11}$) and combinations of these genes that are available.

Resistance selection based on tuber tests should be initiated on the clonal collections at both Peru and Mexico. Emphasis should be placed on determining the degree of correlation between tuber and foliage resistance.

For the recognition of pathogenic shift the following studies may be made: 1) Continue the unsprayed and sprayed plots with the resistant clonal collection and record tuber yield differences; 2) Expand this program to other locations; 3) Make objective measurements of the disease and changes in aggressiveness of the fungus; and 4) Check and analyze old Toluca data.

To study "weak" links in the complex of field resistance: 1) Inheritance studies (the study of inheritance of components of field resistance has been contracted by CIP with the Swedish Seed Association, Svalov); 2) Influence of R-genes; 3) Influence of environment, temperature, light, rainfall, humidity, nutrition, etc.

The following studies on mechanisms of resistance are needed: 1) Resistance to entrance by the pathogen; 2) Resistance to invasion; and 3) Relation between tuber resistance and leaf resistance. Parts 1 and 2 are included in the Svalov linkage contract.

## SOURCES OF RESISTANCE

### Status of Knowledge

The species Solanum Demissum has served as the major source of resistance

currently being used throughout the world in programs of breeding for resistance to late blight. Though originally used as a source of a series of independently acting, dominant R-genes, the species has yielded an even more important series of multiple genes which act to give increasing levels of field resistance to all strains that have evolved to infect R-gene-resistant plants. The highest level of this quantitative resistance approaches that given by R-genes to incompatible races though no plant with this type of resistance escapes the disease, particularly in the Toluca Valley of Mexico. The largest collection of clones with field resistance is maintained in Mexico (1300+).

Current and past work indicates that many of the Solanum species other than S. demissum carry high levels of field resistance. Some species such as S. bulbocastanum are not yet available for use because of inability to transfer the resistance genes through crosses to S. tuberosum, is being studied intensively through a CIP linkage contract with Cornell University, as not only a source of new blight resistance genes but also as a source for other factors such as higher yields and better quality. Solanum phureja also offers a potential additional source of blight resistance as do many of the other tuber bearing species. Though the level of field resistance in the currently large collection of S. demissum - derived clones is very high and offers much immediate hope for control of late blight throughout the developing world, it seems only wise that the additional sources of resistance in the various Solanum species should be incorporated into the collection of resistant germ plasm.

In regard to the demissum-based collection of CIP in Mexico it is apparent that it is too large for practical handling. The pedigrees of the clones should be examined and those having the same sources of resistance and less desirable tuber qualities should be discarded or their characters stored in botanical seed. In addition, those selections with highest resistance and best tuber qualities should continue to be mass crossed to provide a true seed source of wide genetic diversity for use in programs of developing countries and to preserve the genetic traits for future use. Special controlled crosses can and should be made for special problems when requested.

Current information indicates that levels of resistance rated 3 or better (based on the Toluca system of scoring) will be needed to reduce the loss from late blight in developing countries. The 3 level is only moderately satisfactory and levels of 2 or 1 would be much more effective. However, at present the best commercial types of resistant clones mostly have only the 3 level. There seems to be no genetic problem of increasing the level of resistance and maintaining good tuber yields and quality, for such types are now present in some breeding programs.

When a country has the facilities and personnel ready to begin a patato improvement program, the program can move much more rapidly if that country can easily receive vegetative tubers as the source of resistance. If this can be done the primary source of resistance would be selected clones from the Toluca collection, but, in addition, clones with commercial qualities and high field resistance should be imparted from national breeding programs of other countries. In time, as the sources of

resistance from other species become available in clonal stage, they too can be introduced if needed.

If there is difficulty in clonal introduction then botanical seed of crosses with these clones can be received. Selections for resistance and commercial qualities can be made from these families. Currently there is some danger of introducing the spindle tuber viroid in true seed and precautions to prevent this will be needed.

As resistant material is selected for introduction, in so far as possible resistance to other diseases of importance to a country should be present along with blight resistance. Though of major importance in most developing countries, blight resistance alone will not solve their potato device problems.

There is conflicting evidence today as to whether or not tuber resistance is combined with field resistance in the foliage and additional studies of this association are in order. Though reports indicate that tuber rot is less important than foliage blight in most developing countries, the source of foliage resistance introduced should also carry tuber resistance when possible. This gives more security of a tuber crop being present under the resistant vines.

Some discussion is being held as to whether or not field resistant sources void of R-genes should be distributed to a country. At present R-genes are scattered throughout the demissum-derived sources of field resistance, and it would be difficult to avoid them. Also, there is lingering doubt among some breeders that if the R-gene type of resistance is completely removed the level of field resistance would be lessened. As the CIP program progresses, attempts can be made to determine whether the very high levels of field resistance exist in clones without R-genes and these used to develop material for distribution.

## Proposed Program

Maintain, in reduced numbers, clones with the genetic sources of resistance now in the Toluca Valley collection - mostly S. demissum sources.

Incorporate sources of resistance of other species into the germ plasm base now in Toluca, and transfer these sources into breeding material easily used by leaders of projects in developing countries.

Prepare quantities of true seed for distribution, both through mass pollination procedures and controlled crosses.

Arrange to obtain the best blight resistance in good tuber clones of breeding programs in other countries for inclusion in the CIP collection at Toluca, or arrange with such programs to introduce them directly into the developing country.

Combine resistance to blight with resistance to other diseases in the same clones.

Begin to collect information on the level of tuber resistance in the Toluca collection.

Begin to develop, if possible, highly field resistant material void of R-genes.

## BREEDING METHODS

### Status of Knowledge

Methods of breeding for resistance to late blight currently in use by the leading potato breeding programs of the world have succeeded in producing good or adequate levels of field resistance together with the added temporary additional major "R" gene protection. These types of resistance have been primarily derived from Solanum demissum, and they cannot readily be separated. Thus, most breeders have continued to use both types although the ideal is to develop high levels of field resistance alone, but it is not yet known if high enough levels are feasible for most situations. The determination of field resistance in the presence of major genes is done at Toluca, Mexico, the best known place for this because of the high incidence of the disease and the presence of the two compatibility types that are needed for the sexual stage of the pathogen, which presumably permits the ready formation of many races and their preservation in the field in the form of oospores.

Additional sources of resistance are known, and especially interesting is Solanum andigenum which appears to have an entirely different set of genes that can be easily incorporated into commercial type cultivars.

Clones with resistance and high quality that exist in some programs may be useful elsewhere. Selection from progeny of crosses between some of these may readily yield the needed clones which can, by rapid multiplication techniques, become widely grown in a 5-year period. An adaptability problem may be day length sensitivity.

There is a need for a standard rating system to evaluate late blight that could

be readily used. It should therefore be pictorial and simple to interpret.

Proposed Program

Different sources of resistance should be combined.

Resistance sources should be evaluated for as many characteristics as possible so as to make the most suitable clones available according to the needs of each location.

Seed of superior crosses should be made widely available.

The capacity of national programs to receive these materials must be improved or developed when the need exists.

Late blight tests must be conducted first at a national or regional level. Regional testing locations should be promoted.

Results of national or regional tests should be compared with subsequent tests at Toluca to assess their relative value.

A standardized rating system for late blight evaluation should be prepared that incorporates visual aids, but that essentially follows the system now in use at Toluca.

Evaluations at Toluca by CIP personnel should be at approximately 8-day intervals from the inception of blight on the standard susceptible (Alpha) until it is dead. Data for both the susceptible and resistant (Atzimba) standards will continue to be included. Meteorological information should be included in the reports.

Yield information should not be routinely taken, but may be supplied upon special request for multiple tuber clone entries.

Additional help to breeders using the Toluca test should be given when possible by making the crosses or selfs they may request, using detached stems in the greenhouse. Open pollinated seed may also be saved. When crosses with "quality parents" are desired, these may be sent and should be sprayed for blight control prior to crossing.

Since breeder's rights may pose problems with the distribution of the better entries in the Toluca test, it is recommended that breeders should be given two alternatives: 1) Sign an agreement that when they submit clones for testing that these are of a category that is available to anyone qualified and interested; 2) Submit clones that will be unavailable to others but forsake the possibility of being a recipient of clones from other sources in the program. It is further suggested that CIP consider

making it a requirement that all materials be shared, to the benefit of breeders throughout the world, especially in the developing world. All materials must be considered free for use in crosses. Note: CIP policy on this issue has been defined as follows. Since the funds CIP receives are specifically designated for providing assistance to the developing world, all testing done at CIP expense will require that the interested party sign an agreement granting CIP permission to use the materials tested in its program to help the developing countries of the World. The naming of varieties is not a CIP objective, so that no tested clone could be selected for varietal release by CIP (15 October 1973, E.R.F.).

## THE FUNGUS

### Status of Knowledge

The most important characteristic of P. infestans having a bearing on the development of resistant varieties is its extreme variability. The literature documents well the story of the rapid appearance of new pathogenic races which render the R-gene resistance ineffective. The question now of most concern is whether or not the plastic character of the fungus will allow it to overcome the resistance controlled by the series of multiple genes providing the quantitative resistance commonly referred to as field resistance.

The principal modes of variation recognized today are mutation followed by selection, and sexual recombination. The latter as a factor in nature is known only in Mexico. The planning group recognized that the sexual stage is not necessary and probably has little effect on the development of R-gene-specific pathogenic races because of many records of rapid collapse of all known R-gene resistance in regions of severe blight development where the sexual stage does not exist. The rapid development of pathogenic races through asexual variation is usually attributed to random mutation. Some evidence exists that asexual pairing may occur leading to recombinants and possibly different races. Also, some thought is being given again to the hypothesis of host-induced variation.

The stem infections of young plants at the soil level, the infections of leaves touching the soil, and the recovery of the fungus from soil in which potatoes were not grown in the previous two years suggest that oospores play an important role in the survival of the fungus in Mexico. The presence of oospores in the soil at plant emergence may provide an immediate inoculum with the full range of pathogenic races from recombination of the race characters present in the population. The process of evolving complex races

through the sexual stage would be short-circuited. If there is slower evolution to increased aggressiveness to overcome field resistance, the sexual stage would store that level of aggressiveness for continuing the upward change in aggressiveness during the next cropping season.

Mexico studies have also shown that both the $A^1$ and $A^2$ compatibility types occur in all sections of the country so far surveyed. At present the $A^2$ type has not been found outside of Mexico. Thorough search for the $A^2$ type has not been made in other Central and South American countries but should be done because of the reasons noted in the above paragraph. Meanwhile, extreme care in movement of potato parts from without Mexico should be continued.

Race surveys of the past have indicated that the population of races in a country or region may be influenced by the R-gene make-up of the potato varieties being grown. Thus it is believed that detailed race surveys in new countries would serve no useful purpose and that the information gained through use of the R-gene differential hosts would be sufficient. As breeding incorporates whole new pools of genes for resistance into the genetic material being distributed it is possible that studies of race development will need to receive attention. Further it is believed that maintenance of an extensive set of physiologic races for identifying the R-genes in a potential new variety would not now be a function of the Center.

Proposed Program

Stimulate studies to determine whether or not the fungus will increase in aggressiveness.

Encourage the continuation of the studies now going on in Mexico on the role of the sexual stage in survival and the epidemiology of disease development.

Survey other countries of the world especially Central and South America for the occurrence of the $A^2$ compatibility type.

As new gene pools from other species are included in the Center's collection, begin observations for the occurrence of additional sets of pathogenic races to correspond with the resistance genes of the new pool.

Should it become evident through some of the suggested future research, that some major genes (R-genes) are not overcome in the Toluca test, consideration should be given to the value of maintaining a collection of specific races to overcome these R-genes and using them to inoculate spreader rows in the field at testing time.

# ADAPTATION TO DIFFERENT ENVIRONMENTAL CONDITIONS

## Status of Knowledge

The expression of field resistance varies with numerous factors such as the age of the potato plant, the age of the leaf (or its position in the plant), moisture factors (rainfall, relative humidity, soil moisture), temperature, source of origin of the plant, planting density, nutrition, daylength, light intensity, and the presence of viruses (recently shown to reduce late blight incidence).

Considering some of these factors, there is concern that some clones are more susceptible under the short day conditions of the late blight test at Toluca when they are of long day origin. This greater susceptibility is in the form of larger lesions, which may reflect the shorter life span induced in the plant. Day length and temperature factors are considered to interact. In general, temperatures favorable for the potato, are also favorable for late blight. High light intensity appears to increase the resistance of S. tuberosum.

The factors that control field resistance interact with the environment, hence field resistance may vary with each set of conditions.

## Proposed Program

Coordinate observations of late blight incidence on the differential sets at locations differing in day length.

Observe the range of adaptability of Phytophthora infestans in the studies of adaptation of the potato to more extreme temperature conditions (frost resistance, adaptation to the lowland tropics). Differential host sets should be included.

Study the effect of varying conditions during the late blight test, e.g. nutrition, plant density.

Daylength insentivity should be sought and used.

Other methods of controlling late blight should be studied and applied, such as cultural practices (high ridging for tuber rot control) and other methods of control such as breaking the inoculum availability cycle. The progress in chemical control should be monitored, particularly the research and development activities with systemic fungicides.

## ASSISTANCE TO NATIONAL POTATO IMPROVEMENT PROGRAMS

### Proposed Program

Make available resistant materials. The best clones in terms of resistance and quality amongst those in the Toluca collection are available for immediate shipment to requesting programs. Usually about 10 clones are sent, and 10-15 requests are handled per year. These clones may be of adequate commercial level for some situations, thus requiring only multiplication. Shipments should be made in accordance with the regulations of the recipient countries. Tuber desinfestation by chemical treatment is the normal practice, and these materials are free of detectable viruses. When quarantine regulations make introductions to a country difficult, the utilization of regional centers may be useful.

In addition to using the clones of the CIP collection an effort should be made to locate varieties from sophisticated programs that may be useful to others.

For future distributions, consideration should be given to the selection of clones with very high field resistance and no major genes, and to combining different sources of resistance. These should be crossed with clones for desirable characteristics for particular locations (resistance to other diseases, skin and flesh color) or generally desirable characters (high dry matter, high protein, high yield). These materials could be distributed as botanical seed to locations that can screen the segregating populations, or could be grown out and screened for one or more characters and the tubers sent to locations that can utilize them. The blight differentials should be included at such locations.

Develop the capacity to receive materials. Locations that lack adequate programs should be helped in the task of establishing them or improving the ones they have. Present or future potato program members should be trained at CIP or other specialized potato training schools and in the field as a part of CIP's outreach function. It is essential that programs have a designated leader and a defined structure to be effective. Adequate facilities must also exist or be developed.

Seed Programs. Even the best varieties have little impact unless an adequate seed multiplication program exists that maintains the good health of these and makes them available to farmers. The training of seed specialists and the promotion of good seed programs is essential.

Interaction with other programs. The Center should provide guidance to bilateral aid programs to ensure they are best equipped to succeed, and should try to utilize the progress made by successful breeding programs to help others, utilizing the International Late Blight Test as the avenue of approach.

## PROPOSED PROGRAM

### Outreach and Development

The outreach function of CIP is to make available the late blight resistance sources in existance and to help national programs integrate these into their improvement programs.

Resistant clones available in the Toluca collection will be made available for shipment to national programs that want to test these sources of resistance. Import regulations of the recipient countries must be observed. Tuber disinfestation by chemical treatment will be practiced, and these materials will be free of detectable viruses. Regional centers will be established and introductions of suitable clones through these will resolve some of the quarantine regulation problems that exist. Clonal materials will permit a breeding project to get underway rapidly. True seed will also be available, and an increasingly wider source of resistance genes will become available (see Maintainance and Development of Resistance Sources).

The development of national programs to evaluate and utilize materials, and to improve their capacity to do so, are CIP goals. There are many mechanisms by which CIP can train staff members of national programs so that they can more effectively receive late blight resistant materials. These programs must also have adequate facilities.

Seed programs capable of adequately multiplying and maintaining new resistant varieties free of other diseases are essential. CIP conducts seed production training programs at both its Peruvian and Mexican facilities.

### Testing for Blight Resistance at Toluca.

The international late blight testing program, that was conducted under auspices of the Rockefeller Foundation during many years, will continue to be carried out by CIP for as long as it provides a service to plant breeders that cannot be fulfilled effectively by more simple, less costly means. The Toluca valley offers the most stringent blight test known in the World, and will be available for final evaluations of selections made by screening at national (and when possible regional) sites. Regional testing sites will be promoted by CIP, and their relative value assessed by comparison with Toluca.

To improve the test, a standardized rating system for late blight evaluation will be developed (or an existing one selected) that incorporates visual aids and essentially follows the system so far in use at Toluca. Evaluations will be made at approximately weekly intervals from the inception of blight on the standard susceptible (Alpha) until about 2 weeks after it is killed and data on this standard and the resistant standard

(Atzimba) will be reported. Also meteorological information for the period will be included. Yield information will not be routinely taken, but may be requested for multiple tuber clone submissions. Additional help to breeders, such as the execution of requested selfing and crossing, will be provided when possible.

Since CIP's objective is to assist the nations of the developing World, all testing done will be upon the condition that the materials tested can be used by CIP for that purpose.

Maintenance and Development of Resistance Sources.

The large collection of resistant clones in the Toluca collection will be reduced in number - these contain mostly S. demissum resistance genes. The best clones developed by breeding programs around the world will be added to this collection. Any new sources of resistance found in CIP programs in Peru will be included in the collection; those developed by others will be requested. This collection will be evaluated for as many characteristics as possible so as to be able to make the most suitable clones available according to the needs of each location.

Various combinations of resistance and other desirable genes will be developed. Resistance genes from species not presently available in the Toluca collection will be incorporated into more desirable clones more readily usable in breeding programs. Different sources of resistance, including tuber resistance, will be combined. Daylength insensitivity genes will be sought and incorporated into desirable resistance sources. True seed of superior crosses, from both mass pollination and controlled cross methods, will be made available. Desirable combinations of resistance to late blight and other diseases or factors will be produced. The glyco-alkaloid content will be determined in order to avoid clones with high levels for use in breeding programs.

In Peru an attempt will be made to locate highly resistant clones with no major genes, which would reduce the need for testing at a location such as Toluca, and might permit breeding and selection work to be done entirely wherever late blight occurs.

Monitoring Pathogenicity

To assess the pathogenicl potential of the late blight organism (Phytophtora infestans), two standard differential sets will be established, maintained virus-free and distributed: one for field resistance (multigenic resistance) and another for the major R-genes (monogenic resistance).

The field resistance differential clone set will consistof 5 clones representing the five grades of the rating scale among clones adapted to the short daylength conditions of Toluca (selected amongst many clones whose ratings have been previously re-

corded and which will be carefully scored during two growing seasons, and also tested to Race 0 and submitted to qualitative and quantitative inoculation tests) and a similar long daylength set will be selected by North-European scientists (possibly Swedish, Dutch and Scottish).

The major gene differential clone set will consist of the series at Pentlandfield comprising the 12 single gene genotypes r, and $R_1$ through $R_{11}$ plus additional combinations of these genes that are available. CIP is requesting the Scottish Plant Breeding Station to assume the responsibility of maintaining both clone sets and distributing them on CIP's behalf to interested programs around the World.

Since so much responsibility for the success of the Center's programs depends on the multigenically inherited field resistance it is important to know beyond a doubt whether the fungus can also adapt to this type of resistance as it has the monogenic resistance. The accumulated data on blight incidence in fungicide sprayed vs. non-sprayed plots at Toluca will be analyzed to determine if it shows that a shift in aggressiveness of the fungus has taken place. This research will be continued utilizing the more precise rating system that will be developed. The field resistance clone set will be included in future tests, and will be rated in other locations around the world for the same purpose. Studies on the repeated passage of an isolate through clones with different levels of field resistance will be encouraged among collaborators or CIP's own staff.

The role of the sexual stage in survival and the epidemiology of disease development will hopefully continue to be studied by the pioneering Mexican scientists, or by visiting scientists with CIP at Toluca. The presence of the compatibility type A2 will be investigated in Peru, and surveying for it in other South American countries and Central America will be encouraged.

## Field Resistance

Studies on the mechanism of field resistance are being conducted through a CIP linkage project at the Swedish Seed Association in Svalov, Sweden, under the direction of Dr. Vilhelm Umaerus. Emphasis is being placed on 1) resistance to entrance by the fungus into the leaf, 2) resistance to growth of the fungus in the leaf and 3) a reliable method for assessing the possible correlation between leaf resistance and tuber resistance. Similarly, studies on the inheritance of the components of field resistance are being initiated at Svalov.

Additional studies on tuber resistance would be desirable. If there is a correlation between foliage resistance and tuber resistance a method of foliage assessment might be developed which reveals the correlation. This could accelerate breeding programs concerned with tuber resistance. Research on the nature of field resistance in the tuber may be needed to bring this about.

Late blight control.

Research to control late blight by other means than resistance will be considered, such as the value of high ridges for tuber rot control. The progress in chemical control will be monitored, with special interest on the research and development of systemic fungicides.

Adaptation of the potato in relation to blight.

The incidence and significance of late blight will be an integral part of CIP research programs on the adaptation of the potato to environments beyond its recognized normal range (e.g., lowland tropics). The differential host sets will be included at these research sites. Information will be requested from collaborators receiving these sets so as to accumulate information on their response to differing daylength.

APPENDIX I

Background Paper for the

Late Blight Project Planning Conference of CIP

Vilhelm Umaerus

July, 1973

This paper has been prepared on request by CIP to serve as a background for discussions during the late blight planning conference in Mexico City, August 22-27, 1973. It is not my intention to present a complete and up to date review of the present status of research concerning the late blight organism and its host, merely to mention those aspects I feel relevant for the discussions and to give a framework for what should be discussed.

Although references are mentioned not all statements or informations are supported by producing names of authors, neither is there a list of references. I think most of us are familiar with the references mentioned. The term field resistance is used in the way potato people have communicated so far, I think there is no danger of misunderstanding although horizontal resistance may be the more legitimate term.

During the course of the work questions have arisen and I have forwarded those to some of the participants of the meeting. I think the answers are of great interest for the discussions. Therefore they are presented in extenso at the end of the paper. I am most obliged to Dr. WILLIAM BLACK and Dr. MANNON E. GALLEGLY for their replies.

<u>Introduction and justification.</u>

The potato late blight fungus, <u>Phytophthora infestans</u>, is known as the causal agent of one of the major diseases of the potato crop. The fungus probably originates from Mexico and its surrounding countries; now the distribution of the fungus is for all practical purposes coincident with that of the potato itself.

A vast expense of money and labour goes each year on control measures - blight forecasting, spraying with fungicides, haulm killing, production of disease free tubers, breeding of resistant varieties - in those countries, which can afford such measures. Chemical control measures are too expensive for most developing nations especially when the crop is produced by subsistence cultivators. In tropical and subtropical regions blight epidemics are occasionally catastrophic. In some regions, such as Mexico and East Africa, heavy blight attacks may prevent potato cultivation in a number of districts, where it would be possible with the use of resistant potato varieties, adapted to these areas. In other regions the major loss from blight is the loss of the whole of the second half of an otherwise ideal potato growing season. In all of the potato growing regions of South America late blight is a major concern as it is in India and Pakistan.

The breeding of resistant varieties seems to be the only possible way of control of the disease in developing countries, and several breeding programs are now in progress. The world wide interest in the development of late blight resistant varieties is demonstrated by the fact that 29 countries have in the past utilized the field testing facilities in the Toluca Valley of Mexico for determining field resistance to late blight. Those countries are: Argentina, Australia, Bolivia, Brasil, Canada, Colombia, Costa Rica, Chile, Denmark, East Germany, Ecuador, England, France, Guatemala, India, Ireland, Japan, Kenya, Netherlands, New Zealand, Pakistan, Peru, Poland, Scotland, Soviet Union, Sweden, Uganda, United States, West Germany.

Late blight and brown rot (bacterial wilt) are the two major diseases, which must be controlled for adaptation of the potato to the low land tropics. CIP has recently, in a potato bacterial wilt project planning conference, adopted a scheme for developing bacterial wilt resistance, including late blight tests (originally developed by the Wisconsin breeding program).

The breeding of late blight resistant varieties seems to be the only possible way of control of the disease in developing countries and several breeding programs are now in progress. The breeding work has so far met with certain difficulties mostly because of the variability in pathogenicity of the fungus. Race specific resistance, although promising in the beginning, is of limited value especially in areas where the fungus is sexually reproduced, but also in other regions this type of resistance has a short life time due to mutations and somatic recombinations. Most potato breeders now primarily breed for field resistance with a secondary interest in R-gene resistance.

A. The host.

1. Resistance in the foliage.

Field resistance. Field resistance has been attributed to such factors as resistance to entrance, and to growth of the parasite manifested in the number of lesions formed, rate of necrosis, rate of advancement of mycelium, intensity of sporulation and generation time. In addition, factors such as the nature of the leaf surface, growth habit of the plant and type of crop canopy produced, which control the persistence of moisture on the leaf surface, may play a role.

Field resistance may thus be regarded as a complex of different factors, the sum of which determines the actual level of resistance to the parasite apparent under field conditions. It is unlikely that determination of any single factor will give an accurate picture of the true level of resistance. On the other hand screening and selection methods will be more adequate and efficient if based on single, well defined, major components of the field resistance complex. A genetic analysis of the inheritance of field resistance requires that the different factors are studied separately.

As a prerequisite for infection of potato leaves, water droplets or films must persist long enough for germination and penetration of the host to take place. Laboratory and field observations have revealed that highly resistant clones develop fewer lesions per plant than others. There is also evidence of a longer minimum inoculation access period in varieties with a low infection frequency.

Little is known of the nature of this effect. The germination of sporangia and zoospores, or the growth of the germ tubes, the penetration, or the establishment of the parasite in the cells of the host may be affected.

When germination and penetration have succeeded the fungus has to establish a food relationship with the host in order to survive. Mycelium grows in the intercellular spaces of the leaf tissue, sending haustoria into adjacent cells, and once a food relationship is established and the microclimatic conditions are favourable, the fungus sporulates, sending sporangiophores through the stomata of the leaf surfaces. The rapidity of this invation of the leaf varies with the variety. Observations on incubation time, lesion size and growth, generation time, and sporulation capacity are the characteristics commonly used for measuring field resistance.

A food relationship has been associated with the amino acid requirements of P. infestans. The apparent shift towards increased susceptibility when tuber production starts has been attributed to an increased protein hydrolysis at the onset of tuber formation, but also to a shift in the total carbohydrate metabolism of the plant.

Several observations indicate the presence in the potato leaf of factors influencing hyphal growth independently of cell necrosis. It is difficult, however, to sepa

rate the effects of food supply from the action of defence of the invaded leaf tissue. The injury to host cells by the invading hyphae leads to the accumulation of phenolic oxidation products which initiates browning. Oxidizing enzymes and their substrates have been implicated in the infection process. A correlation between peroxidase activity and field resistance has been found under certain defined conditions. Ageing, or mechanical detaching of leaves, or flaming of the petioles lead to the accumulation of soluble nutrients in the leaves and also to a lowered resistance. The amino acid accumulation and its influence towards higher susceptibility can also be explained on the basis of polyphenol metabolism, since an increase in the soluble nitrogen - phenolics ratio often lowers the toxicity of the polyphenols.

The physiological and biochemical factors, which influence the development of a blight lesion, are partly understood. It may be concluded that measurements of the rate of development or size of both the holonecrotic and plesionecrotic zone of a blight lesion reflects the competition between the rate of advancement of the mycelium and the necrosis of the host. The sporing capacity measured as number of spores produced per lesion, or number of spores produced per unit area of sporing zone, may be a function of those characters.

Influence of non-genetic conditions. Ontogenesis and light regime (day length and light intensity) have a large influence on the phenotype of field resistant varieties. This will be discussed later.

A considerable predisposing effect of mineral nutrition on field resistance has been reported by several authors. High nitrogen nutrition might under some conditions be associated with increased resistance, probably due to a prolongation of the period of intensive vegetative growth of plants. Susceptibility seen as lesion growth increases at high levels of balanced nutrition, which apparently creates a tissue highly favourable for the growth of the pathogen. The infection frequency is very little influenced by mineral nutrition. Lesion growth and sporulation intensity increase with increased levels of potassium and decreased levels of magnesium. The rate of lesion growth is more strongly influenced by the treatments than the rate of necrosis.

Genetics. Field resistance in hybrid derivatives of the wild species *S. demissum* is controlled by many different genetic factors and inherited in a polygenic fashion. The complex character of field resistance outlined above represents the combined effect of genetic factors controlling these entities. In the course of hybridization and back crossing to commercial varieties to improve quality and yield these factors become dispersed with consequent reduction in degree of resistance. A detailed genetic analysis of the components of field resistance has not been made, however, a valuable working tool for genetic studies will be the production of dihaploids.

Stability of field resistance. The main advantage of the use of field resistance is that no sudden breakdown is to be expected. The complex expression of field re-

sistance is a guard against sudden changes in P. infestans. Stability of field resistance depends on the buffering effect of the multigenic inheritance of this kind of resistance which counteracts the critical effect of the flexibility of the agressiveness of P. infestans. Still the adaptation of the fungus to a dominating potato variety is possible. The late TOXOPEUS drew attention to the increase in disease attack in the old varieties Champion and Voran with increased acreage of the variety in question. Experience from the long term field testing in Mexico indicates no sudden changes of field resistance although in certain lines some decline has been observed.

Resistance due to hypersensitivity. At the beginning of this century Dr. SALAMAN at Cambridge and his colleagues could demonstrate that wild species were promising sources of resistance. S. demissum was employed in breeding experiments and proved to have a powerful series of resistance genes. Selections from this material remained free from blight for a number of years, but then they suddenly appeared susceptible. It was found that new races were easily produced by the fungus.

The results obtained from the first four R-genes and the sixteen different combinations of them showed that resistance of this form could only be of temporary value. Specialized races to match each gene combination were quick to appear. The R-genes thus failed to provide a permanent solution to the blight problem.

During the years of primary interest in breeding for hypersensitivity much knowledge has accumulated of the biochemistry and genetics of this type of resistance. European and Japanese workers have studied in detail the rapid death of an invaded cell or group of cells when the mechanism of hypersensitivity has been triggered by the infecting fungus. With the decreased value of the hypersensitivity reaction in breeding work this work will not be reviewed here.

Four genes for resistance were originally recognized in breeding material derived from S. demissum. Each gene is inherited independently in a monogenic-dominant manner. These genes were designated as $R_1$, $R_2$, $R_3$, and $R_4$. Including the recessive genotype 16 combinations are possible and differential host series of those 16 genotypes have been used for the identification of equivalent races of the pathogene. Five new R-genes from S. demissum have been identified, which has expanded the possible combinations to 512. Several isolates previously designated as specific races on plants with the original four R-genes were found to have additional genes for pathogenicity. Now genes $R_{10}$ and $R_{11}$ have been recognized, which increases the number of combinations above 2000.

Genes similar to the R-genes obtained from S. demissum have been found in other Solanum species, e.g. S. stoloniferum, S. bulbocastanum, S. pinnatisectum, S. polyadenium.

2. Sources of resistance.

All present evidence point to the Mexican Solanum species as offering the

best prospects in blight breeding. In Mexico and adjacent countries, both the parasite and its hosts have lived in close contact for a very long time with optimum prospects of the development of the complex of genes through natural selection necessary for a stable resistance. Although genes conferring resistance of the race specific type are very frequent they do not seem to contribute to the resistance necessary for survival of those species.

S. demissum is of outstanding value as a source of field resistance both concerning a low infection frequency and resistance once the fungus has entered the host. It is readily crossed with tuberosum and has been used more or less intensively by many breeders, originally as a source for R-genes but with a growing interest as a source of field resistance. Also the diploid Mexican species (S. phureja, S. verrucosum, S. pinnatisectum, S. cardiophyllum, S. trifidum and S. bulbocastanum) have attracted interest from potato breeders.

In several of these species there seems to be no clear distinction between a hypersensitive reaction to infection and one indicating a high degree of field resistance. Several reports indicate the possibility that, when no perceptible lesions are found, the fungus could have been completely excluded from the plant. The possibility of the existence of extreme resistance (not to be confused with race specific hyper sensitive reaction) is not inconceivable in view of the fact that resistance to entrance (measured in infection frequency) is a factor with continuous variation from very high to very low, including none, number of infections.

Sibbing or selfing apparently improves the degree of resistance in the progeny over that of the parents of several of those species. Therefore a certain amount of "prebreeding" within the wild species might be desirable before hybridization with commercial tuberosum varieties. The potentials of breeding on a diploid level especially for the accumulation of polygenes affecting resistance has been advocated by PELOQUIN and HOUGAS, applicable to induced dihaploids of S. tuberosum but also to natural diploid specied. Although those wild species undoubtly have a high value as sources of resistance, some of them may not be so easily available as breeding material because of difficulties in hybridization with S. tuberosum. The work of HERMSEN in Holland and several others to overcome this difficulty with S. bulbocastanum is promising.

While the Mexican potatoes are a major source of genes conferring resistance to blight, a certain fairly low level of field resistance is to be found in some species from the South American continent. Certain selections of S. tuberosum subsp. andigena and S. phureja of the Colombian potato collection have been reported to have a higher level of field resistance than clones of S. tuberosum. A certain degree of resistance has been reported by ROSS in S. commersonii, S. commersonii subsp. malmeanum, S. tarijense, S. acaule, S. spegazzinii, S. curtilobum, and S. tuberosum subsp. andigena, but not of a very high order. ROSS and ROWE have found resistance in three lines of S. microdontum subsp. gigantophyllum. Although some of those wild species carry R-genes as for instance S. vernei and S. kurtzianum the majority of them have resistance

of a polygenic, non-specific type. Attention has also been drawn to andigena through the work at Pentlandfield. According to Dr. MALCOLMSON some of the parents derived from andigena now in use in a general breeding program is contributing towards field resistance. Laboratory and glasshouse studies on detached leaflets indicate some resistance to spread of P. infestans and its sporulation in leaves. The stems, however, appear to be extremely susceptible. Through the years Dr. MALCOLMSON has observed that infection with complex races of P. infestans gives a reaction similar to a major gene resistance, but without segregation suggesting major genes.

3. Breeding methods.

While breeding for hypersensitivity creates few problems in selection and evaluation work this has become a matter of major concern when breeding for field resistance. The ideal field resistant potato would be a variety with a low infection frequency combined with slow mycelial growth, rapid necrosis and low sporing capacity. The complex nature of field resistance and the predisposing effects of ontogenesis and environment must be taken into consideration in the selection work. It is also of importance to consider the requirements of the breeder for quick, reasonably accurate screening methods preferrably in early stages of a breeding program, and with possibilities of handling large amounts of material at low costs. The work should be integrated with selection for other characters, e.g. yield, quality, resistance to other diseases. Observations which are tedious or influenced by plant variation and environment should preferrably be postponed until later in the program when a lower number of breeding lines would be handled and more plants per clone available.

The screening test which is practiced in Svalov is based on the finding that plants with a low infection frequency also require a long inoculation access period (period of free water on the leaf surface and optimum temperature for spore germination and penetration) and that this character is manifested in the young seedling stage. The screening operates very similarly to the screening for hypersensitivity but is made on older plants and inoculum is prepared from races with a broad host range.

Selection for post infectional factors needs much more elaborate techniques and should preferrably be made in subsequent clonal generations. Methods of screening clonal selections for field resistance with emphasis on the post-infectional factors have been practiced in Scotland, West Virginia and Colombia to mention a few places. Glasshouse grown plants are inoculated and incubated in humidity chambers and visual disease index measurements of the progress of the disease form the basis for the selection. Prerequisites for successful testing are:

a) a large number of individual plants per clone,

b) standardized growing conditions especially concerning soil fertility,

c) use of races of P. infestans which would overcome R-gene resistance.

For detailed analyses of post infectional factors (fungal growth rate, rate of necrosis, generation time and sporing capacity) more or less complicated tests have been used either on detached or attached leaflets. Some workers have relied on single tests, others have made several different tests. The more characters included the more elaborate is the assessment and the fewer clones can be handled. On the other hand, accuracy may increase with more detailed studies. LAPWOOD in England analysed four criteria:

a) fungal advancement estimated by measuring the radius of a lesion in mm up to the perimeter on the chlorotic area,

b) extent of sporulation measured in mm of the sporing annulus,

c) intensity of sporulation measured by visual rating,

d) stem and petiole infection from inoculation of leaf axils.

All post infectional factors are considerably influenced by the level of mineral nutrition.

A rapid biochemical test method would be of great value for the assessment of the post infectional factors of field resistance. The peroxidase activity test has offered some promise in this direction. A positive correlation has been found in S. tuberosum, valid also under the predisposing effects of light, leaf age, virus infection and certain mineral nutrition requirements. There is no definite proof that the peroxidase activity is directly related to or being the functioning mechanism of resistance.

Japanese workers (SAKAI and TOMIYAMA) fear that a high peroxidase activity in leaves may be an indication of late maturity. Since late maturity is closely correlated with resistance, they do not believe in a direct relationship between peroxidase activity and disease resistance. Although in general field resistant varieties are late in maturity there are differences in field resistance within the late maturity group. Besides, field resistant varieties have been found also in early maturing material. The correlation between field resistance and late maturity may have historical reasons as pointed out by van der PLANCK. Under natural field conditions early maturing varieties usually escape blight epidemics. Late maturing varieties have to face the full strength of the epidemic and therefore have been under considerable selection pressure.

Field selection can only be made under sufficient epiphytotic conditions. This is difficult to achieve when R-genes are introduced in the breeding material and the compatible races are not present. As mentioned earlier breeders from many countries have taken advantage of the uniquely severe blight environment in Mexico.

The selection for an assessment of field resistance can then be carried out in the following way:

a) in the seedling stage screening can be made of plants with a low infection frequency, that is plants demanding a long period of conditions optimal for infection. This does not include the post infectional factors.

b) in subsequent clonal generations preferrably when selection for other characters has reduced the number of clones, selection is made for rapid necrosis and low sporing capacity either by screening in a glasshouse or in the field under sufficient epidemic conditions or by using biochemical methods.

c) final checking of advanced breeding material and varieties is made by
   1) assessments under field conditions provided that compatible races occur naturally or can be introduced artificially or,
   2) by assessments under laboratory conditions with determination of infection frequency by use of a quantitative inoculator and determination of postinfectional criteria such as lesion size and sporing intensity.

One serious difficulty in selection and assessment of field resistance is the presence of R-genes. Since most of the field resistant selections at the moment are bred from S. demissum it is unavoidable that R-genes are involved in such material. R.genes also occur in S. vernei, S. kurtzianum and S. stoloniferum as mentioned earlier. There is no question about the value of those R-genes when they are functioning. They do however cause difficulties in assessment of field resistance when no compatible races for the particular R-gene is available.

There are two ways of avoiding this difficulty. The first is not to use material with R-gene resistance. As mentioned before many of the South American species may have field resistance without R-genes involved. That would simplify screening and evaluation work in many locations. The second way is to assure the existence of compatible races of the fungus. This can be best achieved in Mexico which is a breeding ground for the fungus and the only place where the fungus is known to sexually reproduce.

MOOI has had experience of the complication of R-genes with the Dutch variety Multa, which originally was thought to possess a good degree of field resistance. However, two years after the release Multa was grown on a larger acreage than before and conditions for development of late blight were favourable. A new race of P. infestans appeared capable of attacking this variety. It was later described as race 1, 4, 10 and Multa had the gene $R_{10}$ with a low level of field resistance.

MOOI also reports that much of the Dutch breeding material has in its parentage resistance factors $R_3$ and $R_{10}$. However, races available in Holland or Scotland have not the combination of pathogenicity factors 3 and 10 and it is thus very difficult to assess the level of field resistance in this material.

The Dutch variety Prevalent is $R_{10}$ genotype. It was sent to Toluca Valley in 1971 and ranked as highly resistant. However, in these areas of the Netherlands where race 1, 4, 10 was found Prevalent was also attacked and found to be less resistant than Alpha. This might indicate that also in Mexico not all compatible races are always available. MOOI suggests that all efforts should be made to promote a spread of compatible races in the testing field in Toluca.

4. Adaptation to subtropical and other climatic conditions.

A number of observations suggest a variation in susceptibility to the disease with age of the potato plant. According to GRAINGER the potato plant shows two periods of susceptibility, one in the very young stage and another later, separated from the first by a period of vigorous foliage development characterized by resistance to late blight. The intermediate partial resistance coincides with the time of the most rapid growth of the plant. At this time before the start of flowering the plants contract the disease only in the lowest leaves. At a later stage, corresponding approximately with flowering time, a change appears and the upper leaves gradually become susceptible. The increased resistance during the period of active growth of the foliage has been associated with slow growth of the parasitic hyphae after invasion but no change in rate of necrosis of the invaded tissues.

A correlation between field resistance and late maturity has been discussed by several authors. Many late maturing and field resistant varieties will have a prolonged period of vegetative growth with development of new axillary shoots. While the leaves of the main stems can be attacked quite early by blight and newly developed secondary shoots will be severely damaged, newly developed axillary shoots remain green with only a few sites of infection. A relationship between late maturity and field resistance seems obvious but does not exclude the combination early maturity and resistance. Many breeders claim to have such varieties. The combination late maturity and resistance is more pronounced in pure tuberosum material, than it is in hybrids with e.g. S. demissum.

A short day treatment of the potato accelerates its rate of development. Under very short days no or only a few axillary shoots are produced and no flowering occurs. Tuber formation starts early even in usually late maturing varieties, and haulm maturity is hastened. A short day treatment also renders usually field resistant varieties susceptible to late blight.

In general photoperiod and ontogenetic predisposition seem to work in parallel. The hastening of development and ageing of the plant is not, however, the only reason for the effect of day length conditions of susceptibility to P. infestans. Inoculation experiments made by the author on potato clones grown under growth chamber conditions at photoperiods of fourteen hours and continous light showed a marked effect on the susceptibility to blight. The difference in time of tuber set and maturity between the two photoperiods was very small, and both could be said to act as "long day conditons". Considerable differences however were found in chemical composition. The main difference was a lower percentage of dry matter in leaves of plants grown under a fourteen hour day,

while the gross composition of the dry matter was fairly unchanged. The data indicate that metabolic changes caused by the difference in photoperiod, but with little or no visible result in the rythm of development of the plant, still cause considerable differences in susceptibility to P. infestans, susceptibility differences which can not be explained by ontogenetic predisposition.

It is possible to stimulate the long day response by treatment of plants with gibberellic acid. Gibberellins may also influence the germ tube length of spores of P. infestans. It has been observed by British workers when studying the infection of leaves by P. infestans that on resistant cultivars long germ tubes were produced before penetration in contrast to the immediate production of appressoria after germination on susceptible varieties. Exposure to short day conditions also gives a considerable decrease in natural gibberellins.

In northern Europe blight develope fairly late in the summer while in East Africa, e.g. Uganda, blight comes very early and kills a susceptible crop before it has bulked. BLACK finds little difficulty in breeding field resistant clones adopted to short day conditions and higher temperature in Kenya. Those clones which are too late for Europe seem to give best results. They probably have a degree of field resistance of such a dimension as to still be sufficiently resistant under short day conditions and behave with normal cropping features.

Blight tests under short day conditions ranks the material more susceptible than it is under long day conditions. The field testing in Mexico is often found to be too severe for material intended for North European conditions. This can be avoided if the interpretation of the readings is based on experience from previous tests.

A sound base would be to have a set of standard varieties adapted to different climatic conditions tested under various blight conditions (including Mexico). Also needed is a standard assessment key used by all breeders not only for assessing leaf area destroyed at a certain moment of attack but also for grouping varieties into different categories of field resistance. Although in general the accordance between blight readings in different countries (including Mexico) seems good, exceptions occur. WURSTER reported that some varieties known to be resistant were severely attacked in Uganda during growing seasons with heavy blight.

## 5. Tuber resistance.

The need of tuber resistance to go along with foliage resistance has often been mentioned by breeders and pathologists. A variety highly susceptible in the leaves may be killed very quickly in a blight attack and a big mass of spores are produced within a short time, but the tubers may hardly be infested at all. A resistant variety on the other hand, keeps the fungus alive for a long time in a very inconspicuous way and the

production of spores may go on for a long period. With no resistance of the tubers those may be damaged to a large extent. TOXOPEUS compiled data from several years of studies of more than 250 varieties on their tuber and leaf resistance. Although there was an obvious positive correlation, there was quite a large number of varieties which were highly susceptible in the leaves but moderately resistant in the tubers. Most observations on tuber susceptibility and resistance are taken from field experiments, but reliable results depend on a good blight attack in the foliage, suitable weather conditions as well as soil conditions.

Screening methods for tuber resistance requiring few replicates have been suggested mainly along two lines. One group of tests measure the infection frequency after spraying of the undamaged tubers or pipetting inoculum on to the eyes. Another group of tests measures the rate of mycelial growth through the internal tissues of the tuber.

A test of the latter type has been described by LAPWOOD, who inoculated slices of medullary tuber tissue of a standard depth and as a criterion of resistance estimated the extent and density of aerial mycelium on the uninoculated surface after a number of days, or the time taken by the fungus to grow through the slice on to the other side. LANGTON has recently described the combination of the two groups. The criterion of resistance in his method was the frequency of infected cores of tuber tissue inoculated through wounded eyes combined with the average time taken by the fungus to appear on the uninoculated surface. LANGTON claims to have good correlation with field observations.

Experiments with unwounded tubers indicate that varieties very susceptible in the tubers under field conditions contract more infections especially through lenticels than do very resistant ones. Tubers of some tuber resistant varieties may develop many infections but the lesions will be arrested when still necrotic threads or after limited rotting of tissues. According to LAPWOOD the amount of rotted tissue separates susceptible from resistant varieties better than do numbers of tubers infected.

Tuber resistance has been found to increase with maturity. This has been attributed to changes in resistance of lenticels and not of eyes.

Changes in the content of phenolic acids and the activities of peroxidase and polyphenol oxidase have been associated both with the healing process after wounding and after infection with P. infestans. The content of phenolic acids increases after wounding and after infection. The increase is greater in resistant than in susceptible varieties. Peroxidase activity is increased, but the increase in polyphenol oxidase activity is still more pronounced especially in resistant varieties. SCHOBER believes that P. infestans is stopped by a layer of suberine in the cell wall and the oxidation products of the phenolic acids in the cell. The ability of the tuber to synthesize suberine and oxidation products such as quinones after wounding and infection are probably of greatest importance in the mechanism of resistance to tuber blight.

However, other factors as indicated by LAPWOOD and associates, may also have influence on tuber susceptibility and resistance. The amount of sporulation in

the foliage differs greatly between varieties, with effects on the concentration of inoculum that reaches the tubers. The "run off" of rainwater from foliage depends on the growth habit of the variety; stem infections are common in some varieties and favours production of spores on a surface readily washed by rainwater. Tuber distribution in the ridge differs, some varieties from tubers on long stolons, others are clustered at the stem base.

RENWICK has recently in an alarming report hypothetically discussed the presence of a teratogenic substance in blight infected potato tubers connected with two abnormalities in human beeings: anencephaly and spina bifida cystica. BOYD has not been able to verify that a correlation exist between the frequency of blighted tubers and the malformations in babies examining Scottish data. Of major concern to us, however, is that RENWICK also claims that there might be reason to suspect substances involved in the resistance mechanism to be teratogenic. From some selected papers he draws the conclusion that solanidine glycosides play a part in resistance to blight. Another group of antifungula compounds are the phytoalexins, which are synthesized by certain varieties in response to infection by certain strains of P. infestans. Those have been identified by Japanese workers as rishitin and phytuberin. There is at the moment no experimental evidence which, if any of those compounds, the solanidine or phytoalexins include the actual teratogene.

B. The fungus.

Two mating types have been described in P. infestans designated as $A^1$ and $A^2$. $A^2$ seems to be restricted to Mexico while $A^1$ has been found in North America, Western Europe, the West Indies, (and according to a personal communications by Drs. J. Galindo and J. Niederhauser also in Brasil, Colombia, Peru, Japan and parts of Africa). Both mating types thus exist in Mexico and are usually present in a ratio near 1:1. They are compatibility types, and not morphological sex types. Each isolate is bisexual but self-incompatible. The degree of maleness and femaleness varies; some isolates of each compatibility type act as strong males and some as strong females, some being intermediate in relative sexual strength.

When gametangial hyphae from the two compatibility types approach each other on lima bean agar usually hyphal attraction is seen. When they meet, the oogonial hypha penetrates the tip of the antheridial hypha. Gametangia formation can also be induced by the Trichoderma method. Only one compatibility type is needed and the offspring is the result of selfing.

In a recent paper SANSOME and BRASIER report that in crossed as well as selfed material two nuclear divisions normally occur in the gametangia, and thus normal meiosis occur prior to gamete formation. The chromosome number from counts of first metaphase configurations is 16 – 20 (2 x (9 $\pm$ 1). According to these date P. infestans is diploid in its vegetative state.

There has been, however, some controversy whether the asexual stages are haploid or diploid. Most of the species of the Oomycetes that SANSOME has studied have been homothallic specied of Phytophthora. There has been some speculation whether the homothallic species are diploid and the heterothallic species are haploid. The present results of SANSOME and BRASIER are supported by the cytological findings of GALLINDO and ZENTMYER in their work with the species P. drechsleri which also appeared to be diploid in its asexual stages. Results from inheritance studies, however, indicate more strongly a haploid state.

With increased interest on developing varieties with a high degree of field resistance the thrust is to have a more stable type of resistance. Although no drastic changes in pathogenicity on field resistant varieties have occurred for several decades the report of GALLEGLY showing presence of aggressive isolates of P. infestans highly pathogenic on field resistant tomato varieties is alarming.

Several investigations give evidence of intraracial variation in aggressiveness among isolates of P. infestans . It is well established that isolates lose aggressiveness after prolonged culture on artificial media. Aggressiveness can be restored after culturing of the isolate on leaves or tubers of the variety from which it has originally been obtained.

Evidence also points to the fact that isolates with several R-gene specific genes are less aggressive than isolates with few or none of these genes. Passage through a susceptible host usually results in the disappearance of the complex races. The build up from an isolate with one pathogenicity factor to several, e.g. race 1 to race 1,4 has also been described.

The mode of inheritance of pathogenicity is at the moment very controversial. Mutation is generally accepted as the mechanism giving rise to new race characters. $R_4$ genotypes frequently appear spontaneously in almost any pathogenic isolate of P. infestans . Very few have succeeded, however, to induce mutations artificially. If P. infestans is diploid in its vegetative state, as the cytological studies of SANSOME indicate, recessive mutations will not be expressed in the original colony, which may explain the failure to induce mutations artificially.

DENWARD, and independent of him, BENNET are of the opinion that extranuclear entities, structures that can be defined as episomes, may replicate and distribute in the hyphae. CATEN and JINKS suggest that variation in rate of growth and sporangium production is under cytoplasmic control.

## C. Expected contributions of CIP.

In the late blight program of CIP priority should be given to projects intended to create a basis for rational blight resistance breeding. One of the reasons

for the planning meeting, is to discuss and put forward questions, which have not been solved and need attention. Those questions may fall in various fields, e.g.:

1. The saving of genetic material of potential value for future late blight resistance breeding at the moment in danger of genetic erosion.

2. A better understanding of late blight resistance, its mechanisms, inheritance and factors influencing its expression.

3. The continuation of the international late blight test in Mexico and the most efficient way to make use of the material and knowledge available there for the future.

4. The extension of knowledge, experience and material to national breeding programs interested in blight resistance.

## ADDITIONAL COMMENTS

To stimulate the discussion I formulated a few questions, which were sent to Dr. BLACK and Dr. GALLEGLY. These are the questions and the answers:

a) Both of you have supervised in the potato work in East Africa (Kenya and Uganda), and interesting presentations of this work were given at the meeting in Lima last year with particular emphasis on late blight resistance. Do you find the present germ plasm and the level of resistance it contributes sufficient for future breeding in East Africa? If not, should CIP give priority to search for field resistance to blight in the germ plasm available to the center?

BLACK: "We have a wide range of breeding material in Kenya and we can produce group I and group II resisters in reasonable quantity. We are releasing a new variety at the moment which reacts somewhere between groups I and II. It looks very promising in every way, e.g. yield, size, shape and cooking quality. It has not yet been tested in Mexico, but the screening results of progenies bred from it, indicate field resistance without the interference of R-genes. Nevertheless, I would suggest that CIP should examine the material they have and try to improve upon what is already available."

GALLEGLY: "Dr. WURSTER and I found that the levels of multigenic resistance present in our breeding program gave excellent performance in Uganda. The same was true for this type of resistance in clones from the programs of Mexico, Netherlands, Scotland, etc., tried in Uganda. Thus there is sufficient resistance to significantly contribute to the East African programs. I personally believe that this type of resistance will be stable in most areas where late blight is a factor. The major job to be done is the one of selecting resistant clones adapted to the particular geographic area which give high yields and have good quality. Meanwhile the Center could well benefit by identifying commercial-type clones with resistance as well as accessions of Solanum species with resistance for trials in a country to begin the selection process. The first approach in a new program would be to start with named varieties and clones approaching variety status. If needed then one could turn to the species."

b) Do R-genes still contribute to the value of blight resistance or do they create more problems in screening and evaluation of field resistance than merits their existence?

BLACK: "Since R-genes are commonly found in selections bred from S. demissum, it could be difficult to get rid of them without losing good breeding material. Their presence could protect a variety completely for some years and if that variety is known to be moderately field resistant, the advent of new races should not be very serious. In other words, field resistance must be present, and if effective R-genes are also present they would give added protection for a time."

c) What is your experience of the adaptation of field resistant clones to the particular environmental conditions in East Africa? A strong influence of daylength is often mentioned with a lower level of field resistance under short day. I learned from WURSTER that blight comes very early in Uganda. What effect has that on breeding for resistance?

BLACK: "I find little difficulty in producing field resistant clones adapted to short day conditions and higher temperatures. Types that are too late in maturing for Europe seem to give best results. We are trying some in the lowland tropics to see if they ar also tolerant to high temperatures."

GALLEGLY: "There is strong circumstantial evidence that the expression of multigenic resistance is influenced by day-length and light intensity. I believe that day-length effects are really those effects that influence maturity, and the resulting influence of increasing maturity on reducing the expression of resistance. Low light intensity also will reduce the level of resistance as indicated in greenhouse studies, and all of us in certain areas of the United States have seen multigenic resistant plants with a lot of blight following a few weeks of constant cloudy, rainy weather. During the rain periods in Mexico and Uganda I observed as a usual condition the clouds, the rain, and bright sunshine in between geographic areas. Thus, a breeding program is most effective when selections for day-length adaptability and resistance are made under the local conditions of the potato growing regions of a country.

In some of our work cooperatively with Niederhauser in Mexico we have identified a few clones that are resistant in Mexico and susceptible in Maine and West Virginia. The reverse is the usual case. When a clone is resistant in the Toluca Valley in Mexico it usually is also resistant in Northern U.S. The few exceptions probably are interrelated with day-length and maturation."

d) The Toluca Valley, Mexico, has been a valuable testing ground for breeders from many countries. Do you have need for this testing ground for future work?

BLACK: "R-genes can be a nuisance in screening for field resistance if the appropriate races are not available. They can completely mask the degree of field resistance present by giving a hypersensitive reaction. When such plants are tested in the Toluca Valley there seems to be every chance that the necessary races will be present to give the true picture. For that reason I think the trials in the Toluca Valley should continue."

GALLEGLY: "Toluca Valley is probably the best site in the world for a "late blight proving ground." The advantages are numerous. Diversification of tuber-bearing species and concept of the "home of the potato", whether it is or not,

applies to this site. The fungus has been in the presence of diverse host germ plasm from the beginning and thus should be developed to its highest order of pathogenicity. The day-length characteristics are closer to those of most tropical areas yet experience has told us that most selections with resistance are even more resistant in northern hemisphere areas (I do not know about performance in the southern hemisphere). Experienced staff and adequate facilities have been developed over a period of years at this site."

e) Have you information on the accordance between blight readings in Mexico and other locations?

BLACK: "I have some clones that have been tested in Scotland, Mexico and Kenya and the results are more or less comparable. In general, the higher temperature in the tropics seem to favour the fungus and give slightly larger lesions, but the difference is not big enough to cause concern. As Dr. WURSTER said, blight can come early and kill a susceptible crop before it has bulked, but even a group III resister would yield a crop in the same conditions - although it would benefit from spraying with fungicide! "

GALLEGLY: See c)and d)above.

f) CIP has a rather intensive parental breeding program on bacterial wilt resistance. Do you find it feasible to have a similar program for late blight?

BLACK: "Resistance to bacterial wilt is a much more difficult problem than resistance to blight because good, highly resistant clones are not available and a simple, reliable, method of screening progenies has not been devised. By comparison, the blight problem could be regarded as more or less under control."

GALLEGLY: "I believe I have essentially suggested this approach above for a Center program.. This may not be a parental development program per se but the identification of clones and accessions with resistance which a country could secure for their first-step trials. Some of these may be named varieties, and from the collection it may be possible to quickly relieve the situation of that country. There is the problem of introduction of vegetative clones through the plant quarantine facilities of a country which must be overcome. Either disease free clones or true-seed lines may be needed. CIP might later do the actual crossing using parents identified from the first-step trials as having qualities approaching those desired in a country. The true seed could be sent to that country relatively easy."

g) Dr. GALLEGLY, you have devoted much work into the field of genetics and cytology of P. infestans. Do you find this to be within the scope of CIP:s program? If so, which particular questions would you recommend CIP to consider?

GALLEGLY: "An understanding of the genetics of host-parasite interactions in the late blight disease and the cytology, particularly the nuclear situation, is important for persons working directly with the Center's programs. I question whether the Center should emphasize this aspect of research on late blight, particularly the cytogenetic area. If the need is felt, perhaps the Center could contract for such studies somewhere in the world where an unbiased approach could be made. There may be some need for direct Center research on furthering our knowledge of the genetics of the disease, and this need might be felt as higher and higher levels of multigenic resistance are introduced into commercial culture. Will this resistance continue to hold in all geographic areas? It is now clear that none of the monogenic factors will hold up in the face of this pathogen, and there is really no good evidence that these qualitative genes serve in an additive manner as seems to be the case with the other quantitative genes which appear to be completely independent. The use of the words "seems to be" and "appear to be" indicates need for generating additional information about the relationship of the two gene systems. Another problem facing us today is whether or not the multigenic resistance is associated with high levels of undesirable edible qualities of tubers as suggested by the hypothesis papers of RENWICK and associates. I think not but the question must be answered. We got into trouble with most of our highly multigenic resistant lines because of very high levels of total glycoalkaloids - much higher than in the variety Lenape which was removed from our marketing channels because of it. Fortunately a few lines were low in TGA & still resistant. What about other chemicals, such as rishitin and chlorogenic acids? Are these compounds teratogenic, and are there other teratogens associated with resistance? The Center would not want to be guilty of improving the quantity and nutritive value of the potato over the world only to find an increase in birth defects as a result."

On my request Dr. GALLEGLY answered other questions of importance:

" I believe that we have reached a plateau of multigenic resistance to late blight, and the real and big job now before the Center is to apply this knowledge in development programs where blight is a factor. This will be a slow process and require a lot of money and energy. Not only will we have to identify sources of resistance in that region, it will have to be incorporated with resistance to other diseases and other desirable horticultural characters. Further, not just one variety will do the job - chip, bakers, [illegible] etc., and early, medium and late varieties. There is a long road ahead in reaching this goal. Meanwhile we should be looking for a higher plateau of resistance and a higher plateau of yielding ability for use much further down the road.

Another more specific study of shorter range might be on correlations of tuber and foliage resistance with the idea of shortening our screening procedures."

Dr. KENNETH D. SAYRE is at the moment on a Rockefeller post doctoral assignment with the International Potato Program in Mexico and has recently submitted to CIP a list of recommendations for future activities of the CIP regional program in Mexico. Dr. SAYRE prefaces his list of recommendation by stating that "they do not call for additional funding or personnel, but provide for a more efficient use of the funds and personnel that are currently available." These are excerpts of Dr. SAYRE's recommendations concerning the late blight work:

a) The International Late Blight Test. Perhaps the most important project that is conducted in Mexico is the International Late Blight Test. Each year several cooperating potato improvement institutions send potato germplasm in tuber form to screen for late blight resistance in the Toluca Valley. The tubers are planted in a quarantined area at the CIMMYT station in the Toluca Valley and regular blight readings are taken. These readings are sent back to the cooperators to aid them in the development of blight resistant varieties. This is the extent of the contribution that is made by the Mexican program. I suggest that more can be accomplished in Mexico to further assist the cooperators.

First, if a cooperator would specify that crosses and/or selfs should be made using the most resistant clones present in his material, this could be accomplished in Mexico using cut-stems. The best resistors can be identified in the field early enough to allow cut-stems to be harvested. A greenhouse is available to make the crosses and I intend to use the balance of money I have left in my Rockefeller grant to install an air-conditioning and humidifying system in the greenhouse to provide more optimum conditions for making crosses using cut-stems. The personnel now working in the program are well versed in crossing techniques. The seed resulting from the crosses or selfs would be returned to the cooperator and should greatly increase the rate of advance of his selection program.

Second, if a particular cooperator has blight susceptible clones that he would like to cross with the most resistant clones in the material he sends, these clones could be planted in a plot that would receive fungicide and the crosses could be made. In this way he will have the hybrid seed at least 6 months earlier than if he had to wait until he received the blight readings from the material he submitted for testing.

Third, the possibility also exists for cooperators to send populations of botanical seed for blight testing. This seed could be planted in the greenhouse during the winter and the seedling tubers would be ready for planting in the field by May for blight screening. Again crosses or selfs, at the direction of cooperators, would be made and the resulting seed returned for selection in the home country. This cycle could be continued until a population is developed with a high level of blight resistance and with maturity, tuber characteristics, and other disease and insect resistances selected for in the home country. I estimate that by staggering the planting of botanical seed in the available greenhouse, approximately 7000 seedlings could be handled each year. In addition, the exchange of botanical seed between the cooperators and Mexico would minimize the quarantine problems in Mexico.

Fourth, many cooperators, who send material to Mexico for late blight screening, use preliminary greenhouse or growth chamber screenings to eliminate a portion of the material undergoing selection. I propose that the late blight test in Toluca could be used to evaluate the effectiveness of these preliminary screenings. The cooperator could conduct his screening as usual but, instead of sending only his selected clones to Mexico for testing, he could send all clones that were involved in the screening process. The proportions of the clones that possess resistance at Toluca in the unselected and selected populations would provide an indication of the efficiency of the screening test.

These four recommendations that I have set forth concerning the conduct of the Internacional Late Blight Test in Mexico represent by no means all of the possible added contributions that could be undertaken. I hope that the late blight workshop scheduled for August in Mexico can provide a forum for the discussion of these and other possibilities.

b) Maintenance of the Germ Plasm Bank of Late Blight Resistant Clones. There areapproximately 1000 clones with varying degrees of resistance to late blight that are currently being maintained by the Mexican program. Of these 1000, approximately 300-400 have an acceptable level of late blight resistance. Some of the other clones have other desirable characteristics and, therefore, should also be maintained. The rest are still present in the bank because of the natural reluctance to discard unique clones.

Last year, I initiated a collection of open-pollinated botanical seed from all clones. We collected seed from about 80% of the clones. This year, all clones were planted and seed will again be collected. Therefore, following this year, I recommend the elimination of those clones that have poor late blight resistance; that do not possess other notable, beneficial characteristics; and for which we have successfully collected botanical seed. The cost of their maintenance does not justify their existence especially since their genetic potential is available as botanical seed. I would like to see the number of clones in the bank reduced to between 600-700 clones. I would, however, like to receive advice from Dr. ROWE concerning this situation. We should look upon this germplasm bank from two viewpoints; 1) as a reservoir of late blight resistance; and 2) as a broad-based population of primarily Tuberosum germplasm. This second viewpoint should have some bearing on whether the decision is made to eliminate certain clones.

I am in complete agreement with the manner in which the germplasm bank is planted each year. That is, 10 tubers of each clone are planted and sprayed with fungicide and insecticide, and 10 tubers are planted and sprayed with only insecticide. This allows a continuous monitoring, over years, of the stability of the resistance of each clone by comparing the fungicide versus no fungicide plots, and the late blight readings from year to year. This date, however, needs to be pulled together and summarized, and kept current.

I would like to see a more conscious effort expended towards the disper-

sal of the genetic potential of the bank. Until last year, only tubers could be distributed (which involved quarantine limitations in many other countries). Now we can also begin to distribute botanical seed. This should be more fully publicized for the benefit of potato breeders around the world.

CIP has contracted a linkage program to Svalov, Sweden, which commenced July 1 this year. The overall objective of this program is to assist the International Potato Centers in the back-ground work needed for the development of late blight resistance in the national potato breeding programs of the developing countries. Five major goals have been recognized and the procedure to assist the Center in this work is outlined in a proposal which has been accepted by CIP. The five goals are as follows:

1. To cooperate in studies of the germ plasm available to the International Potato Center in search for sources of field resistance.

2. To conduct studies on the mechanism of resistance with emphasis on:

   a) resistance to entrance of the parasite into the leaf;
   b) resistance to growth of the parasite in the leaf (lesion development);
   c) relation between leaf resistance and tuber resistance and the influence on other tuber characters, e.g. cooking quality.

3. To conduct genetic studies, concerning the inheritance of components of field resistance.

4. To cooperate in studies of the adaptation of field resistant clones to temperate, subtropical and tropical conditions with emphasis on the expression of resistance.

5. To extract information from the above mentioned goals with influence on development of methods of selection, evaluation and other aspects of breeding potatoes resistant to late blight.